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By EDWARD C. JEFFREY, B.A. (Tor.), Ph.D. (Harv.)

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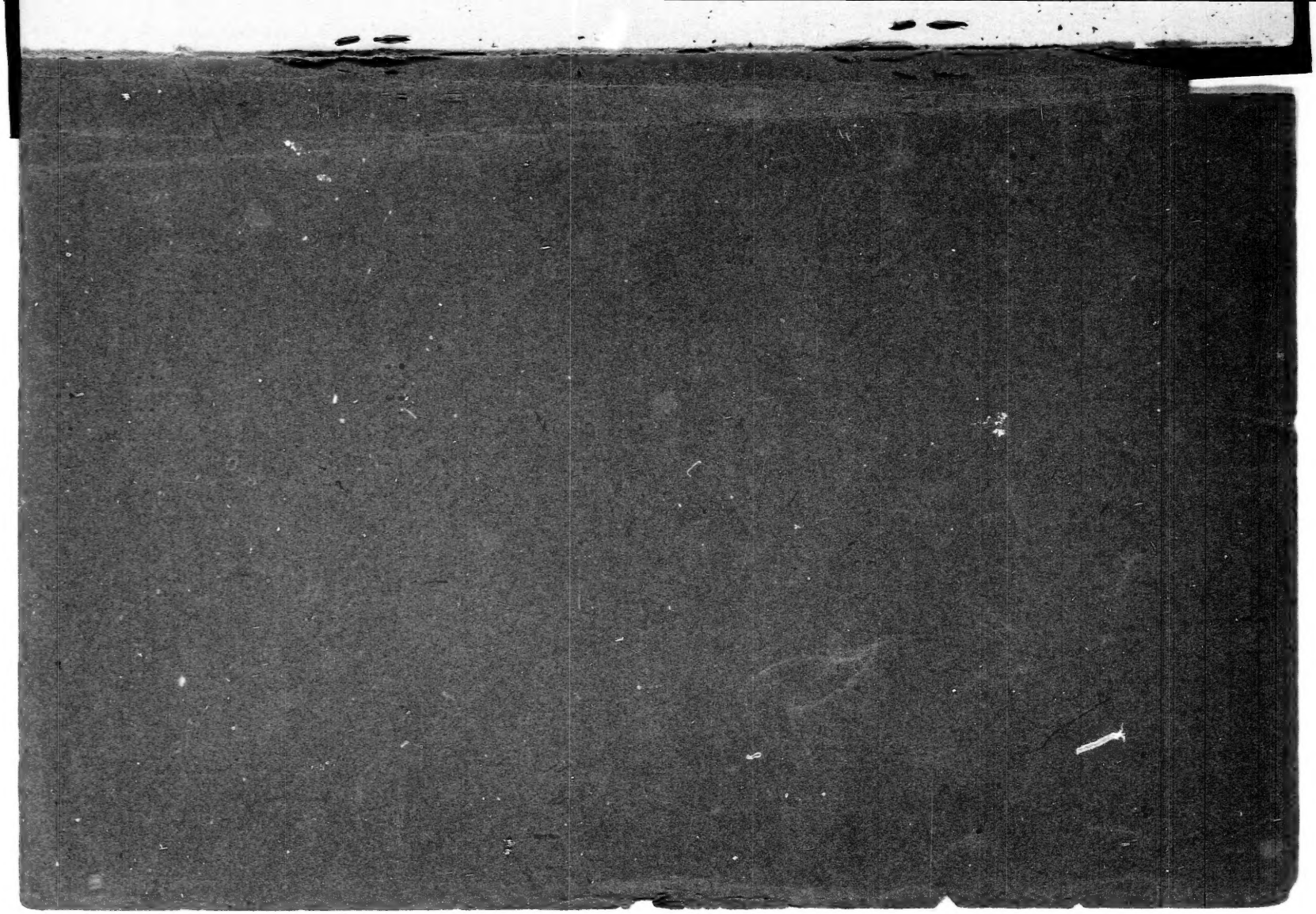

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The prevailing views in regard to the morphology of the vascular apparatus of the higher Cryptogams and the Phænogams are due to the studies of Van Tieghem and Strasburger. Both these writers have abandoned the conception of fibro-vascular strands, which is embodied in the classic comparative anatomy of De Bary. In this treatise, the axial organs, primary and secondary, of the higher plants are regarded as composed of more or less modified fundamental tissue of a parenchymatous nature, bounded externally by the integumentary tissues of the epidermis and traversed by conductive strands typically composed of vessels and sieve-tubes. These fibro-vascular strands may consist of clusters of xylem and phloëm placed side by side, and in this case the strands are called collateral fibro-vascular bundles. In another type the phloëm surrounds the xylem, and the bundle is then described as concentric. The latter type, by the localization of the phloëm at intervals on the outside of the xylem, becomes the radial bundle.

As a result of his study of the anatomy of the stem of the phænogamous order, Primulaceæ, Van Tieghem[1] published in 1886 an important memoir on the morphology of fibro-vascular strands, which has formed the basis of most of the subsequent anatomical work in this direction. Although the general conclusions reached are founded on the study of the Primulaceæ alone, Van Tieghem extends them to all vascular plants, including the vascular Cryptogams. The primitive type of axis, according to Van Tieghem, contains but a single concentric fibro-vascular strand, which is limited externally by a specialized layer, the pericycle. The innermost stratum of the fundamental tissue, immediately adjoining the pericycle, is also differentiated from the outer cortical tissue and is named the endodermis. The fibro-vascular axis so delimited is called the central cylinder or stele. This sort of fibro-vascular axis is found in the stem of many Cryptogams and in the root of nearly all vascular

1 Sur la Polystélie. Ann. de Sci. Nat. Bot., 7 sér., tom. 3.

plants, both cryptogamous and phænogamous. On account of the fact that the stele or central cylinder in such axes is obviously single and undivided, they are designated monostelic.

According to Van Tieghem the monostelic central cylinder is sometimes modified by becoming expanded. The stele grows larger, and a certain amount of the stelar parenchyma becomes aggregated in the centre to form the medulla or pith. From the pith, strands of parenchyma radiate outwards towards the pericycle and constitute the medullary rays. These parenchymatous rays divide the xylem and phloëm into segments, designated meristeles or bundles, which, in his opinion, are morphologically very different from the concentric bundles of De Bary. The pith and the medullary rays are also of a different morphological origin from the extracylindral fundamental tissue of the cortex. The whole complex medullated central cylinder of this type is shut off from the cortex by the same two layers, *viz.*, the pericycle and the endodermis, as is the primitive non-medullated concentric fibro-vascular strand. This modification of the central cylinder is found in the stems of nearly all the Phanerogams, and, in isolated instances, among the Cryptogams, *e.g.*, the Osmundaceæ, the genus Botrychium, and certain species of Equisetum.

In the medullated monostelic axis, the endodermis and pericycle, according to Van Tieghem, sometimes bend inwards between the meristeles and break into pieces at the bottom of the sinuosities. The fragments of the thus interrupted pericycle and endodermis unite around the inner side of the individual bundles, which they in the first place merely subtended. The original medullated monostelic central cylinder is considered to become, as a consequence, astelic, since its pith and rays are imagined to become continuous with the fundamental tissue outside the stele. The astelic type of central cylinder is found in certain amphibious or limicolous phænogamous orders and among the Cryptogams in the genus Ophioglossum and certain species of Equisetum. In these cases the separate meristeles, each surrounded by its own pericycle and endodermis, may unite so that a more or less complete fibro-vascular ring is formed, bounded both externally and internally by a continuous pericycle and endodermis. The central cylinder is then said to be gamodesmic. For example, in the genus Equisetum, *E. limosum* and *E. litorale* have the individual meristeles completely surrounded by an endodermis and pericycle; in the rhizome of *E. silvaticum* and in the aerial shoots of *E. hiemale*, on the other hand, the meristeles are fused together and the ring of united meristeles is bounded both outwardly and inwardly by a circular endodermis.

Instead of expanding and becoming medullated monostelic, or passing from this modification into the astelic condition, the fibro-vascular axis, may, according to Van Tieghem, undergo successive bifurcations and thus become polystelic. This type of central cylinder is very prevalent among the vascular cryptogams, and occurs also in certain species of Primula and Gunnera among the Phanerogams. In a cross section of an older stem of this type, numerous concentric fibro-vascular strands are to be seen imbedded in a matrix of fundamental tissue. The originally separate steles of the polystelic axis, may unite, according to Van Tieghem, to form a concentric annular stele, which is described as gamostelic.

More recently, Van Tieghem[2] has returned to the subject of the central cylinder of the Equisetaceæ. In his essay on Polystely, he describes the central cylinder of *E. arvense*, *E. pratense*, etc., as medullated monostelic; *E. limosum* and *E. litorale* as astelic, and the aerial shoot of *E. hiemale* as gamodesmic. Confirming an earlier research of Pfitzer,[3] he recognizes that in the species originally described by him as medullated monostelic, viz., *E. arvense* and *E. pratense*, etc., there are, in the region of the nodes, and at the basis of the smaller branches, well marked indications of an internal endodermis, which disappears in the internodes, only to recur in the successive nodes. He concludes that it was primitively present throughout the entire length of the stem, and has become in these species vestigial, persisting only at the nodes. He expresses the opinion that the astelic type of central cylinder, as found in *E. limosum*, is the primitive one, and that by fusion there resulted the gamodesmic type found in the aerial shoots of *E. hiemale*, and the subterranean stem of *E. silvaticum*. Forms like *E. arvense*, *E. pratense*, and *E. scirpoides*, are also gamodesmic, although the fact is obscured by the partial degeneracy of the internal endodermis. As a result of this investigation, it is apparent that the medullated monostelic type of central cylinder does not exist among the Equisetaceæ, and that those species which at first sight appear to possess a stelar system of this type are really degenerate astelic gamodesmic. The writer has recently studied the development of the young stem in the Equisetaceæ,[4] and has shown that the stelar system in the young axis of this group, is primitively gamodesmic, possessing a well-marked, continuous, internal endodermis. The modification, in which the bundles are surrounded by individual endodermal sheaths, appears quite late in the development of

2 Remarks sur la Struct. de la Tige des Prêles. Journ. de Bot., 4, 1890, p. 365.

3 U. d. Schutzscheide d. Deutsch. Equiset., Jahrb. f. wiss. Bot. 6.

4 Mem. Bost. Soc. Nat. Hist. Vol. 5, No. 5, p. 171.

the young sporophyte. If any dependence is to be placed on ontogenetic results, it would appear that the primitive type of cauline stelar arrangement in the Equisetaceæ, is not one in which the bundles are surrounded by individual endodermal sheaths, but is, on the contrary, that designated by Van Tieghem as gamodesmic. The appropriateness of this term, as describing the conditions present in the young stelar system of this group, will be discussed subsequently.

Van Tieghem[5] has recently re-examined the central cylinder of the Ophioglossaceæ, as a result of the discovery made by Poirault[6] of the occurrence of an internal endodermis in the *young* stelar system of several species of Botrychium and Ophioglossum. He confirms Poirault's results and describes the distribution of the endodermis in the young central cylinder of *Botrychium Lunaria*. The stelar system is tubular, and above the point of origin of the first leaf-trace has an internal, as well as an external, endodermis. The inner one rapidly disappears in the older region of the young stem. A similar state of affairs occurs in *Ophioglossum vulgatum*, although in this case, the stelar tube becomes quickly broken into separate strands on account of the overlapping of the foliar gaps. The endodermis in this species also disappears in the older region of the stem. Poirault[6a] has described a somewhat persistent *internal* endodermis in *O. Bergianum*, *O. capense*, and *O. ellipticum*. Quite recently an internal endodermal layer has been described by Farmer[7] as occurring in the interesting genus Helminthostachys. His own observations, together with those of Poirault, lead Van Tieghem to the conclusion that the cauline stelar system of the Ophioglossaceæ is, above the exit of the first leaf-trace, astelic in the sense already defined. It is apparent also, although Van Tieghem does not call attention to this fact, that the primitive condition of the fibro-vascular tissues in the stem of this group, is gamodesmic in his sense, and in this respect, corresponds with that described by the writer as existing in the young stem of the Equisetaceæ.

The recent investigations of Van Tieghem and Poirault apparently make it impossible to regard the central cylinder of the Equisetaceæ and Ophioglossaceæ as in any sense, monostelic. *Equisetum arvense*, the genus Botrychium and the genus Helminthostachys, which were described by Van Tieghem in his essay on Polystely as belonging to the latter type, are shown by a more complete study of their anatomy and development to possess a gamodesmic central cylinder (in the sense of

5 Journ. de Bot., 1890, p. 405.

6 Ann. d. Sci. Nat. Bot., 7 sér., tom. 18., p. 169.

6a Op. Cit., p. 169.

7 Ann. Bot., vol. 13., p. 434.

Van Tieghem) in which the internal endodermis has become more or less obsolete. It has further been rendered probable by the interesting investigations of Poirault[8] that the apparently medullated monostelic central cylinder of the stem of the gleicheniaceous genus, Platyzoma, also possesses a pith derived from the extrastelar fundamental tissue.

The only remaining example cited by Van Tieghem in his classic essay on Polystely, of a Cryptogam possessing a medullated monostelic central cylinder is that offered by the Osmundaceæ. The writer hopes to show in a memoir on the anatomy of the Pteridophyta, which will appear shortly, that here too, the pith is in reality an included portion of the extrastelar fundamental tissue.

The medullated monostelic type of central cylinder may accordingly be regarded as of very doubtful occurrence among the Cryptogams, and in those cases where it is apparently present, it is derived from a modification of Van Tieghem's gamodesmic type. There would thus appear to be very slight evidence for regarding the medullated central cylinder, where it occurs among the Cryptogams, as derived from the dilatation of an originally pithless stele. It is a well-established principle with morphologists to attempt always the explanation of the structure of the higher plants by the more easily understood corresponding features of the lower groups. It seems to be in harmony with this method to elucidate the obscurities of the morphological interpretation of the central cylinder in the Angiosperms by the facts derived from the study of the anatomy and development of the Pteridophyta and Gymnosperms. The writer will shortly publish a memoir describing his studies on the latter groups. In the present essay, he proposes to examine in a general way, certain features of the structure and development of the Angiosperms, which in the light of the investigations mentioned above, seem to afford to some extent an elucidation of the morphology and phylogeny of the higher Phænogams.

PROBLEMS.

The questions to be treated in the present memoir are briefly as follows: Has Van Tieghem correctly described the mode of origin of his polystelic type of central cylinder? Is his astelic type essentially different from the polystelic? Does the medullated monostelic central cylinder ever arise by the dilatation of a primitively pithless stele? What are the salient anatomical features of the central cylinder of the Angiosperms?

8 Op. Cit., p. 182.

Do they throw any additional light on the difficult problems of the genetic relationships of the group? Anatomical studies have hitherto been almost entirely neglected by American botanists on account of the wealth of other matters, and that fact will serve as a sufficient justification for the present research. Were any other needed, it would be afforded by the extremely important phylogenetic results obtained in recent years by English, French, and German palæobotanists from the study of the fossilized remains of the chiefly vegetative organs of various groups of extinct Cryptogams. The advance of the science of Ecology has furthermore made it less difficult to distinguish between those cenogenetic features of structure which are the result of the adaptation of plants to their modern environment and those palingenetic traits which serve as an indispensable guide in the interpretation of phylogeny.

THE POLYSTELIC TYPE.

In his essay on Polystely to which reference has already been made, Van Tieghem[9] describes this modification of the central cylinder as originating from the pithless monostelic type, by the successive bifurcations of the primitively simple stele. He has referred to it more recently in practically identical terms.[10]

In studying morphological problems, it is an accepted method of procedure to pass from the lower forms to the higher. This course has been profitably pursued in the investigation of the morphology of sporangia, anthers, ovules, etc., and in the examination of the homologies of the gametophyte in the various groups of vascular plants. Curiously enough, Van Tieghem has given very little attention to the lower forms in his studies on the central cylinder, and still less to their development. In his essay on Polystely he does not describe the development of any cryptogamous stems of the polystelic type. It is only subsequently in his Traité de Botanique (p. 765), that he makes a slight reference to the development of the polystelic central cylinder of *Pteris aquilina*. Leclerc du Sablon[11] has given an admirable description of the earlier stages in the development of the stem of this species, but has apparently, not correctly observed the later phases.

The writer proposes to describe briefly his own observations on this form, as a preliminary to the examination of the phenomenon of

9 Op. Cit., p. 282.

10 Traité de Botanique, 1892, p. 1370; Élements de Botanique, 1898, p. 179.

11 Ann. Sci. Nat. Bot., 7 sér., 11 Tom., Récherches sur la Tige des Fougères.

Polystely in the Angiosperms. This species is chosen because the investigation of Leclerc du Sablon, and of the writer, show it to be quite typical of the polystelic Pteridophyta. The form selected presents, moreover, the phenomenon of Polystely in a high state of complexity, and its cosmopolitan occurrence will make it easy for other botanists to verify, if so minded, the accuracy of the description given here.

Leclerc du Sablon[12] has correctly described the transitional region of the young stem of *P. aquilina*. Higher up, and immediately above where the first leaf-trace is given off from the concentric central cylinder, the phloëm sends a process into the centre of the vascular axis of the strand. When the gap, caused in the axis by the exit of the foliar tracheids, is closed again, the central phloëm remains included, forming a sort of pith. The exit of the traces of several subsequent leaves causes similar gaps in the continuity of what is now the vascular tube, and through these gaps the internal phloëm communicates with that outside. Photograph 1, plate 7, shows the structure of the young stele, at a point where the second leaf-trace has just passed off. The central island of small-celled bast can be distinguished, surrounded by a ring of tracheids, which is interrupted opposite the leaf-trace, *t*. At the level of the fourth or fifth leaf, the fundamental tissue penetrates to the centre of the stele through the foliar gaps, forming, henceforth, a continuous core within the internal bast. At this stage the stelar system is a hollow cylinder, perforated by gaps above the points of origin of the leaf-traces. Leclere du Sablon[13] correctly describes it as being, in this phase, like the stelar tube, which is permanently present in the stem of Marsilea. The writer has not been able to distinguish any evidence of the repeated bifurcation of the young central cylinder, described by Van Tieghem as characteristic of his polystelic type. On the contrary, both the writer's observations and those of Leclerc du Sablon seem to show that the young stelar system of *P. aquilina* is of the type described by Van Tieghem as gamostelic. That term, however, can hardly be correctly used to describe the structure of the central cylinder of this species, because it implies the fusion of steles, originally separate, of which there is no indication whatever in this form. The writer[14-15] has previously suggested the term siphonostelic as more accurately describing the conformation of the young stelar system in the so-called polystelic Filicales; for his studies on the development of a number of

12 Op. Cit., p. 3.

13 Op. Cit., p. 5.

14 Trans. Brit. Ass. Adv. Sci., 1897, p. 869.

15 Mem. Bos. Soc. Nat. Hist. V. 5, No. 5, p. 160.

representatives of this group have led to the conclusion that the young central cylinder of this type is always tubular, and that there is no indication of the bifurcation of the primitive fibro-vascular axis.

Photograph 2, plate 7, shows the older stelar tube of *P. aquilina*, where it is provided with an axial core of fundamental tissue. At *a* is to be seen the foliar gap corresponding to the leaf-trace l^2; *r* is a root, and l^1 an earlier leaf. When about a dozen leaves have been formed, the vertical young stem of *P. aquilina* bifurcates, or in some cases trifurcates, and the resulting divisions plunge into the soil and pursue a subterranean horizontal course. Leclerc du Sablon[16] has made a curious mistake in regard to the mode of origin of the horizontal rhizome of this form. He describes it as originating from a bud in the axil of one of the leaves of the vertically-growing young plant. The writer has seen the bifurcation of the stem regularly occurring in many hundreds of examples of plants grown from different lots of spores and in different years; so that there can be no doubt that it is a quite normal process. The writer's account, moreover, agrees exactly with the older description of Hofmeister[17]. Photograph 3, plate 7, represents a section of the young stem just above the bifurcation of the stelar system; *a* and *b* are the tubular steles which are about to pass into the two horizontal rhizomes. The stele *a* has just given off a leaf-trace *l*; in *b* the foliar gap is also still open. Shortly after the young rhizomes make their appearance, the leaves, which at first originate at small intervals, become more widely separated, and their foliar lacunæ frequently overlap. For this reason, in a cross-section of the stem at this stage, one often sees an appearance of independent dorsal and ventral steles, as in photograph 4, plate 7. A series of sections, however, show that the stelar system is still tubular. At this stage, a strand of brown sclerenchyma becomes evident in the centre of the stelar tube, and, a few centimetres further on, the ventral wall of the latter becomes involuted. A fibro-vascular strand is subsequently detached dorsally from the involution, and forms one of the two large axial concentric bundles found in the mature rhizome. The single central strand is rapidly surrounded by a sclerenchymatous tube formed from the sclerenchymatous rod described above. This stage is represented in photograph 5, plate 7. Subsequently, a second central strand is detached dorsally from the ventral wall of the stelar tube. This strand is at first small, but ultimately becomes nearly as large as the first-formed strand (fig. 6, plate 7). The two axial concentric strands contribute to the formation of the leaf-traces, but have no connection with the vascular supply of the roots.

16 Op. Cit., p. 5.

17 Higher Cryptogams, Ray. Soc., p. 214.

Possibly misled by Hofmeister's older account, already referred to, Van Tieghem[18] has described the large axial strands as primitive, and the strands outside as secondary cortical steles derived from these. A study of development shows that, in reality, the external strands are primitive, as may indeed be inferred from the fact that the traces of the roots and leaves are directly attached to them even in the mature rhizome. The axial concentric strands, on the other hand, are of later origin, and are to be regarded as medullary bundles.

It will probably be obvious to the reader who has followed the foregoing account and examined the accompanying photographs, that the development of *P. aquilina* offers little support to Van Tieghem's hypothesis of Polystely. The writer hopes to publish in the near future, an account of the stelar development of a number of cryptogamic forms of the so-called polystelic type, in which the arrangement of the nascent fibro-vascular apparatus is identical with that found in *P. aquilina*. The young stelar system of the so-called polystelic type among the Filicales would appear to be characteristically tubular, and the writer[19] has already suggested on that account, that it may be appropriately designated siphonostelic.

PRIMULACEÆ.

Having discussed in a general way the development of the so-called polystelic type in the Cryptogams, we may now profitably turn our attention to the development of the same type in the Angiosperms. It was the study of the anatomy of the stem of a large number of species of the genus Primula which led Van Tieghem to propose the doctrines in regard to the morphology of vascular strands, which are at present so generally accepted by anatomists. Although derived, in the first place, from an examination of certain Angiosperms, Van Tieghem's hypotheses have been extended by their author also to the Cryptogams.

Van Tieghem describes two main types of cauline anatomy as occurring in the Linnæan genus, Primula. In one type, the central cylinder becomes dilated above the cotyledons and forms a medulla[20] This medullated monostelic central cylinder does not subsequently undergo divisions. In a second type the central cylinder remains undilated and without a medulla for several internodes above the

18 Op. Cit., p. 765.

19 Trans. Brit. Ass. Adv. Sci., 1897, p. 869.

20 Sur. la Polystélie, p. 292.

cotyledons, and then bifurcates, repeatedly producing a varying number of eccentric steles.[21] The fibro-vascular system in this case is described as polystelic. Van Tieghem retains, for species possessing a cauline central cylinder of the first type, the original Linnæan generic name Primula; for the polystelic species, he revives Tournefort's genus Auricula.

Van Tieghem does not seem to have followed closely the development of the polystelic type in his genus Auricula. The writer has given some attention to this subject, but it has not seemed necessary to make his studies exhaustive, because an admirable account[22] of the whole matter has recently appeared, with which the writer's own results are in close agreement. Gwynne-Vaughan has examined the development of the young stem and the relation of the leaf-traces to the cauline central cylinder. He calls attention to the fact that the young pithless stele of *P. japonica and P. involucrata* after the exit of from four to eight leaf-traces becomes gamodesmic (gamomeristelic) in the same manner as the central cylinder of the young stem of *Botrychium Lunaria*, described by Van Tieghem. In other words, there is present a collateral fibro-vascular cylinder with an internal endodermis as well as an external one. This cylinder is perforated at intervals by the gaps occurring at the points of exit of the leaf-traces, and around the margins of these gaps the external and internal endodermis become continuous. Higher up in the young stem, the gamodesmic cylinder becomes more or less completely gamostelic by the formation of internal xylem and phloëm. The leaf-traces show the same variability as the cauline strands. In the petioles of the younger leaves they are collateral strands, while in the stalks of the later-formed foliar organs some of them become concentric and would thus be considered, from Van Tieghem's standpoint, as steles.

As regards the nature of Polystely itself, this writer reaches conclusions which are so much in accord as far as they go with the investigations to be described in this memoir, that they may be quoted in full. For example (p. 320) he makes the following statement: "Van Tieghem seems to have entirely overlooked the all-important influence of the leaf-traces on the phenomena of transition, and, indeed, on the vascular system throughout the whole plant. On this account, he regards Polystely, when present, as having originated by the continued bifurcation of the central cylinder found in the lower part of the stem. He speaks of it as flattening itself out, and constricting itself in the middle

21 Op. Cit., p. 305.

22 Gwynne-Vaughan; Polystely and the Genus Primula, Ann. Bot., 1897.

until it becomes nipped into two. I have not seen anything that would lead to a similar conclusion. The transitional phenomena in the seedling and also the extreme variability in certain species of the most important characteristics of Polystely, give strong support to the opinion that Polystely is not a primitive feature of the group of Primulas, in which it is found, but a comparatively recent modification." On a later page (322) he writes: "One result appears clear: that in the Primulas the gamostelic condition is more primitive and nearer normal monostely than is the dialystelic (polystelic) type, and that probably a gamodesmic condition preceded either."

The writer's observations have been made entirely on *P. Auricula* and *P. farinosa*. The so-called monostelic species, *P. sinensis*, *P. obconica*, and *P. Forbesii*, have been studied for comparison. The writer's results in the case of *P. Auricula* correspond very closely to those reached in the same species by Gwynne-Vaughan[23]. As was long ago noticed by Kamienski[24] the epicotyledonary central cylinder remains an unmodified single strand until several leaf-traces have been given off from it. About the region of exit of the fourth or fifth leaf, it becomes a stelar tube with the usual foliar gaps. As soon as the central cylinder becomes tubular, the traces running to each leaf become three in number, the largest of which comes off from the bottom of the foliar gap, while the two smaller lateral traces are derived from the vascular tissues forming the sides of the gap. It is only by following a series of sections that the really cylindrical character of the stelar system can be made out, since the foliar lacunæ overlap and there is thus presented the appearance of completely isolated strands. It is only necessary in this connection to emphasize the statements of Gwynne-Vaughan quoted above, that Van Tieghem has overlooked the influence of the leaf-traces on the conformation of the central cylinder, and that there is no evidence of the repeated bifurcation of the primitive stelar strand, such as he describes for this and other so-called polystelic species.

The writer's study of the young stem of *P. farinosa* has resulted in very similar conclusions. In this case the problem is simplified by the fact that the individual leaves receive but a single strand from the cauline stelar system. In the quite young axis, the stele does not immediately become tubular. Above the point of origin of a leaf-trace, the pericycle sinks into the stele, forming a sort of medulla (photograph 7, plate 8), which may be compared with that composed of both phloëm and peri-

23 Op. Cit., p. 320.

24 Vergleich Anat. d. Prim., 1878., p. 28.

cycle in the young fibro-vascular axis of *Pteris aquilina* (photograph 1, plate 7). After six or more leaf-traces have been given off, the stelar tube encloses a core of fundamental tissue. The internal face of the young stelar tube is at first devoid of phloëm and it is only subsequently that it appears, thus recalling the state of affairs described by Gwynne-Vaughan in *P. japonica* and *P. involucrata*. At this stage the stelar tube would be described in accordance with Van Tieghem's terminology as gamodesmic (gamomeristelic): collateral strands occur even in the old stem; such a strand is figured by Kamienski.[25] Photograph 8, plate 8, shows a transverse section of the stelar system of this species at a region where the internal phloëm has already made its appearance. At r^1, a root is being given off; r^2 is a radical stele which has already made its exit from the central cylinder; l^1 and l^2 are foliar gaps; opposite l^1 may be seen its corresponding leaf-trace. Photograph 9, plate 8, is similarly lettered. In this case the leaf-traces corresponding to two foliar gaps are to be seen. The stelar system of *P. farinosa* is thus from the first, a tube, including primarily only a pericycle, and then fundamental tissue as well. The tube is, in the beginning, collateral, but becomes subsequently bicollateral through the appearance of internal phloëm. The stelar tube has gaps in its walls above the points of exit of leaf-traces. No such gaps occur opposite the outgoing radical strands.

The writer's examination of the development of *P. farinosa* leads to results similar to those obtained by Gwynne-Vaughan in the case of other so-called polystelic species of this genus, *viz.*, 1. That the stelar system in the young plant does not successively bifurcate, giving rise to a varying number of steles, as described by Van Tieghem, but from the first forms a stelar tube with foliar gaps. 2. That the stelar tube is primitively collateral and only subsequently becomes bicollateral; the development of the internal phloëm would seem to be a compensation for the disappearance of secondary growth in the vascular system of these peculiar species of Primula.

HALORHAGIDACEÆ.

The peculiar conformation of the fibro-vascular system of the genus Gunnera has been described by Reinke.[26] Subsequently the central cylinder of *G. macrophylla* has been somewhat exhaustively studied by

25 Op. Cit., plate 6, fig. 3.

26 Morpholog., Abhand. v. Reinke, Leipzig, 1873.

Merker.[27] Van Tieghem[28] examined the anatomy of a number of species of this genus in connection with his essay on Polystely. Certain species, *G. cordifolia*, *G. monoica*, and *G. prorepens* possess monostelic central cylinders which are quite pithless. In these species this state of affairs is sometimes departed from in the leafy stems (as distinguished from the creeping rhizomes) where the stele may occasionally, according to Van Tieghem,[29] flatten out and bifurcate in the usual polystelic fashion. The strands however in these cases are never more than two. In *G. magellanica* and other species, the young stele bifurcates a certain number of times in the epicotyledonary region and becomes polystelic. In species with large stems, *e.g.*, *G. macrophylla*, etc., the bifurcations are described by Van Tieghem[30] as being exceedingly numerous.

Through the quite exceptional kindness of Dr. D. H. Scott, Director of the Jodrell Laboratory, Kew, the writer has had the opportunity of examining material of seedlings of *Gunnera scabra*. As Dr. Scott himself has an article on this species in preparation, it will be possible only to refer in a passing manner to the writer's own observations. All that need be said in this connection is, that the epicotyledonary system of *G. scabra* is primitively tubular, as are those of *Pteris aquilina* and *Primula farinosa;* and that it is further characterized by the same foliar gaps subtending the points of leaf-traces. It resembles, moreover, *Primula japonica* and *P. farinosa*, in the absence of internal phloëm, on the inner side of the young stele. So far as may be judged from the development of these species, the polystelic Gunneras do not differ in the nature of their young stelar system from the other polystelic forms examined by Gwynne-Vaughan and the writer. They resemble the polystelic Primulas in showing developmental evidence that the so-called polystelic condition is derived from a primitively so-called astelic arrangement of the vascular tissues.

SAXIFRAGACEÆ.

The writer has found the so-called phenomenon of Polystely to be present in the Saxifragaceæ. As one of his students is working over the anatomy and development of the stem in this order, it will be necessary only to refer to certain features having an immediate bearing on the present research.

27 Merker, Gunnera Macrophylla. Inang. Diss., 1888, Marburg.
28 Op. Cit., p. 307.
29 Op. Cit., p. 308.
30 Op. Cit., p. 309.

If a transverse section of the internodal region of *Parnassia palustris* be microscopically examined, it will be discovered that the stele is provided with a pith formed of thick-walled collenchymatoid cells. There is considerable secondary growth present in the woody zone traversed by slender medullary rays. The central cylinder is surrounded by a well-marked and lignified endodermis, which appears very clearly after the use of phloroglucin and hydrochloric acid. Most of these features may be seen in photograph 25, plate 11. In a section passing through the point of origin of a leaf-trace, the side of a central cylinder is seen to be hollowed opposite the outgoing trace; at the bottom of the concavity the phloëm and xylem are absent, so that the collenchymatoid tissue of the central cylinder of the stele is only separated from the external fundamental tissue by the pericycle and endodermis. Not unfrequently two leaf-traces come off from the stele, nearly opposite each other, as may be noted in photograph 26, plate 11. When this happens the central cylinder is split for a short distance into two strands. At their lowest point the two strands are devoid of internal phloëm and xylem, and have along their inner borders a layer of the pith-like tissues described above. The latter is separated from the fundamental tissue passing through the stele of this region, only by the pericycle and endodermis. These features may be seen in photograph 27, plate 11. Higher up, the fibro-vascular tissues cover over the internal faces of the two strands again, and they become, to employ Van Tieghem's terminology, two separate steles, each of which apparently possesses a medulla of its own. Photograph 26, plate 11, sufficiently illustrates the description given above. The photograph very closely resembles Fig. 33, plate 15 of *Gunnera magellanica* in Van Tieghem's memoir on Polystely.

The points of interest in the anatomy of this species seem to be that there is present an apparently medullated monostelic axis, which continues as such unless two leaf-traces from it come off close together; that under these circumstances the divided stelar axis becomes at first, astelic, and then a little higher up, polystelic, in Van Tieghem's sense of these terms. It is further to be noticed that both astely and polystely are closely related to the exit of leaf-traces.

In *Parnassia parviflora* the central cylinder is astelic, or rather gamodesmic, since it consists of a collateral fibro-vascular tube with an internal endodermis, which communicates with that outside, through the gaps occurring in the cylinder opposite the points of exit of the leaf-traces. A section of the central cylinder of this species is shown in photograph 29, plate 11: l is an outgoing leaf-trace; g^2 is its corresponding gap, and g^1 is that of an earlier trace; r and r^2 are strands belonging to roots,

which as is usual, cause no gaps in the fibro-vascular tissues, by their exit from the stelar tube.

The foliar vascular strands in both these species are generally throughout their cauline course collateral in structure, but early in their petiolar course, they become concentric. In these features, they resemble the leaf-traces of *Primula japonica* and *P. denticulata* described by Gwynne-Vaughan.[31]

It is undesirable, for reasons already mentioned, to describe further the anatomy of the Saxifragaceæ at the present time, and the subject of Polystely may be left with a brief summary of the writer's conclusions.

From the study of the development of the so-called polystelic central cylinder in the vascular Cryptogams and in the Angiosperms, the writer has reached the following conclusions: (1) Polystely (so-called) does not arise by the repeated bifurcation of the primitive epicotyledonary central cylinder. (2) The young central cylinder of this type is primitively tubular and is characterized by the occurrence of gaps in the wall of the stelar tube corresponding to the leaf-traces. These essential features may subsequently be obscured by the passage of numerous traces to the same leaf, by the overlapping of the foliar gaps of different nodes, and by the development of an internal or external system of strands (or both) derived from the original stelar tube. (3) If the above conclusions be accepted, the terms Polystely and Gamostely should apparently be abandoned, since they involve an erroneous conception of the mode of development of the central cylinder in the various forms described above. The writer proposes as more accurately describing the nature of the central cylinder in this type, the term siphonostelic.[32]

THE ASTELIC TYPE.

In his essay on Polystely, already often quoted, Van Tieghem describes a modification in the central cylinder of vascular plants, which he calls astelic. In this type, the epicotyledonary stele, having previously become expanded and medullated, is said to become further changed by the sinking in of the endodermis between the bundles. In this case, according to Van Tieghem, the endodermis is apt to break at the bottom of the undulations between the bundles, and the thus separated segments then envelope the several vascular strands with

31 Op. Cit., p. 312.

32 Originally suggested in Trans. Brit. Ass. Adv. Sci., 1897, p. 869.

individual endodermal sheaths. By this process the pith is supposed to become continuous with the extrastelar fundamental tissue, and the central cylinder disappears as such.

Van Tieghem states that of closely allied species some may have a medullated monostelic central cylinder, while others have the astelic type of central cylinder. For example, in the Equisetaceæ, *E. arvense* is monostelic, *E. limosum*, on the other hand, is astelic. Among the Phanerogams, *Ranunculus aquatilis* and *R. Lingua* are described as having an astelic central cylinder, while a number of other species, *e.g.*, *R. acris* and *R. abortivus*, are monostelic. In the genus Anemone, parallel cases are presented by *A. nemorosa*, which is astelic, and *A. pennsylvanica* which is monostelic. It has been pointed out in the introduction that Van Tieghem in more recent publications has abandoned the idea that any of the Ophioglossaceæ or Equisetaceæ are medullated monostelic, but, on the contrary, regards them as astelic throughout the epicotyledonary region of the stem. Although he has given up the view that the cauline central cylinder of these Cryptogams is in any case medullated monostelic, he is still of the opinion that certain ranunculaceous genera[33] present examples of both the above-mentioned types of central cylinder.

Before going on to submit Van Tieghem's views in regard to the morphology of vascular strands of certain Ranunculaceæ to the test of their agreement with the facts of anatomy and development, it is necessary to describe certain modifications of these views which have recently been proposed by Strasburger[34] and which have already been accepted by many botanists of eminence. Strasburger admits the great morphological value of Van Tieghem's definition of the central cylinder. He suggests, however, inasmuch as the innermost layer of the cortex which bounds the central cylinder is not always an endodermis, *i.e.*, a layer of cells provided with a cutinized undulating radial band, but is very often composed of sclerenchymatous elements or starch-bearing cells, that some general name is desirable for the internal layer of the fundamental tissue adjoining the central cylinder. He suggests the term phlœoterma as a suitable designation of the innermost layer of the cortex, no matter what its histological character may be. Strasburger questions the possibility of different species of the same genus having in some cases a medullated monostelic central cylinder, and in others presenting the astelic type of arrangement of their vascular tissues. In other words, he believes it impossible that the medullary

33 Éléments de bot., 1898, p. 179.

34 Histolog. Beiträge III, pp. 309-313, 442, 443, 484-486.

tissues should in some species of a given genus be intrastelar and in other species extrastelar. He accordingly regards the phlœoterma which surrounds the whole complex of bundles in the so-called monostelic type as morphologically different from the individual sheaths enclosing the bundles in Van Tieghem's astelic type. Strasburger has apparently overlooked the fact that Van Tieghem[36] had anticipated his objection to the different morphological interpretation of the pith in different species of the same genus, by announcing that in the case of the cryptogamous orders, the Equisetaceæ and Ophioglossaceæ, the medullary tissue is always extrastelar, thus, as has already been pointed out, departing from the view originally expressed in his essay on Polystely. Van Tieghem[36] still maintains, however, his earlier position in regard to the varying morphology of the central cylinder in different species of Ranunculus and Anemone.

We now come to the consideration of the development and structure of so-called astelic axis in the Ranunculaceæ and other groups.

RANUNCULACEÆ.

Our knowledge of the anatomy of this order is chiefly due to the studies of Marié.[37a] Although he has described quite exhaustively the salient structural features of the root, stem, and leaves of this order, he has given little or no attention to the subject of the development of the stem, which, as the writer hopes to show, is of considerable importance from a morphological standpoint. Quite recently Jancezewski[38] has examined the anatomy of a number of species of Anemone. Strasburger[39] attributes to Marié the statement that *Ranunculus acris* possesses a common endodermis (phlœoterma), *i.e.*, in other words, that the central cylinder of this species is medullated monostelic. Marié's description[40] is extremely condensed, and, on that account, is somewhat ambiguous; but the writer is inclined to interpret it as meaning that the bundles of this species have individual endodermal sheaths, since he states that *R. acris* resembles *R. multifidus*, which has individual endodermal sheaths.

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35 Journ. de Bot., 1890.

36 Élements de Botanique, p. 179.

37 Récherches sur la Structure des Rénonculacées. Ann. de sci. Nat. Bot., 6 sér., tom. 20.

38 Révue Générale de Botanique., 1898. Études Morphol. sur le Genre Anemone.

39 Op. Cit., p. 311.

40 Op. Cit., p. 80.

The young stem of *R. acris* has a stelar system very much like that of *Botrychium Lunaria*, *i.e.*, it consists of a fibro-vascular tube pierced by foliar gaps. Through the latter, the internal phlœoterma, which is extremely well marked in the young stem of this species, communicates with the external phlœoterma. Photograph 13, plate 9, shows a leaf-trace passing off from the stelar tube, and subtending it is the foliar gap. The continuity of the internal and external phlœotermal layers through the foliar gap can be easily distinguished. The photograph in this case was made from a section treated with phloroglucin and hydrochloric acid, which causes the lignified phlœoterma to stand out sharply. The stelar tube, as in the case of the young so-called polystelic axes, only becomes fully established after several leaf-traces have been given off, including those of the cotyledons, and at first, as in the young stem of *Primula farinosa*, the tube contains only enclosed pericycle and no fundamental tissue. The leaf-traces to each leaf are originally single, but very soon become three in number: a central large one and two smaller lateral ones. The departure of the median trace causes a large gap in the stelar tube, through which, the internal and external phlœotermal layers communicate. The lateral strands cause smaller breaks in the continuity of the fibro-vascular cylinder and frequently the internal and external cortex do not become continuous through them. The gaps, as a result, are occupied merely by pericycle. The stelar cylinder in the more advanced young stem is characterized by the overlapping of the foliar gaps, so that in a cross section it appears as a circle of separate bundles. This state of affairs is shown in photograph 14, plate 9. Somewhat higher up in the young stem, the overlapping foliar gaps become more numerous, both on account of the increased number of leaf-traces given off to each leaf and the greater elongation of the individual foliar gaps. For this reason, the stelar tube, in transverse section presents the appearance of a number of separate vascular strands, the fibro-vascular bundles, each of which is surrounded by its own phlœotermal sheath. In older regions of the stem, the fibro-vascular strands of the leaf-traces dip inwards and pass outwards again, thus simulating the peculiar course of the leaf-traces which becomes the rule among the Monocotyledons.

From the thick parenchymatous hypogæous stem of *R. acris* the more slender aerial shoots originate. Since the latter must support, in spite of their comparative delicacy, a considerable weight of leaves, flowers, and fruit, the mechanical tissues which are scarcely present at all in the subterranean stem, are well developed in the epigæous shoots. As is well known, the mechanical tissues of *R. acris* appear as fibrous sheaths around the individual bundles. Already, in the older subter-

ranean stem, the internal phlœoterma is less apparent, and at the base of the aerial shoots, both external and internal phlœotermal layers cease to be recognizable as such. This disappearance takes place *pari passu* with the appearance of the sclerified sheaths about the individual bundles. It is highly probable that the outer layer of sclerified cells on the external and internal faces of the bundle-sheath represents the phlœoterma, and that the rest of the fibrous tissue is to be regarded as sclerified pericycle. It is not easy to come to an opinion in regard to the position of the phlœoterma on the flanks of the bundles, but since the larger so-called bundles are completely surrounded by a phlœotermal sheath in the hypogæous stem, it may be safely assumed that the larger bundles of the aerial shoots are to be considered as morphologically bounded by a similar membrane. The smaller bundles in the hypogæous stem are often united with the larger ones by their pericycle; as a consequence, they are surrounded by the same phlœotermal sheath. It seems probable that they are to be regarded as similarly united with the larger bundles in the epigæous shoots.

The development of *R. sceleratus* has been studied by the writer, and does not differ essentially from that described in *R. acris*, in respect to the structure of the young central cylinder and the distribution of the phlœotermal sheath.

The young stem of *R. repens* also resembles closely that of *R. acris* in every respect, both as regards development and the distribution of phlœoterma. In the older stem of this species, the phlœotermal sheath disappears completely in the internodes of its characteristic runners; it becomes distinct again, however, in the rooting nodes, both internally and externally.

R. abortivus is described by Marié[41] as having an external phlœoterma. The development of this species is, accordingly, of special interest. The conformation of the young fibro-vascular tube does not differ in any important feature from that of *R. acris*, and consequently need not be described. The distribution of the phlœoterma in the young stem of this species is, however, of considerable morphological interest. In the lower region of the epicotyledonary central cylinder, an internal phlœoterma is present, which communicates with the phlœotermal layer outside the fibro-vascular tube, through the foliar gaps, in a manner quite similar to that obtaining in *R. acris*, as described above. The internal phlœoterma is somewhat persistent,

41 Op. Cit., p. 82.

and only in rather stout young hypogæous stems does it become quite obsolete.

Photograph 15, plate 9, represents a section through the upper region of the stem of a well-advanced seedling. Phloroglucin and hydrochloric acid have been used to bring out the lignified phlœoterma which can be clearly distinguished on the outer margin of the fibro-vascular segments, but less distinctly along their inner border. The occurrence of an internal phlœoterma in the young fibro-vascular cylinder of a species in which it is absent in the mature hypogæous stem, is of considerable morphological interest. In the aerial shoots, the phlœotermal boundaries are no longer distinguishable histologically, although on morphological grounds they should doubtless be regarded as nevertheless present.

Even in the quite young stem of *R. rhomboideus*, there is no trace of an internal phlœoterma. However, by examining the youngest region of the axis, a quite distinct internal phlœoterma may be demonstrated. Photograph 17, plate 9, represents a cross section of the young stem where the fibro-vascular cylinder appears as an unbroken ring. Photograph 18, plate 9, shows a tranverse section of the stelar tube where it is interrupted by a foliar gap; the junction of the internal and external phlœotermal layer around the sides of the foliar gap can be clearly discerned. Photograph 16, plate 9, represents a section through an older region of the subterranean stem; three foliar gaps are to be seen and the internal phlœoterma has now become quite obsolete. The aerial shoots of this species do not differ materially in the structure of their vascular strands from the other species already described. *R. rhomboideus* is distinguished from all the species examined by the complete disappearance of any histological evidence of the existence of an internal phlœoterma, even in quite young stems. Even here, the boundary of the cortical tissues on the inside of the stelar tube may readily be determined by examining the stem in a very early stage of development.

The writer has not been able to secure seedlings of other species of Ranunculus, but those described appear to be sufficiently varied in their affinities to afford reliable data for conclusions as to the correct morphological interpretation of the central cylinder of this genus. These deductions may, however, be advantageously deferred until the allied genus Anemone, has been considered.

As has been already mentioned, Van Tieghem states that certain species of Anemone have a medullated monostelic central cylinder

while other species are astelic. *Anemone nemorosa* belongs to the latter class and is described by Marié[42] as having the individual bundles surrounded by phlœotermal sheaths. *A. pennsylvanica* has, according to the same author,[43] a continuous external phlœoterma surrounding the whole complex of bundles. The writer's discovery of an internal phlœoterma in the *young* stems of various so-called monostelic species of Ranunculus, has suggested the examination of the younger region of the subterranean axis of this species of Anemone. Photograph 19, plate 10, reproduces a section of the quite young hypogæous stem of *A. pennsylvanica.* The stelar system is interrupted by a foliar gap, around the margins of which the internal and external phlœotermal layers are in communication. Photograph 20, plate 10, represents an older region of the cylinder where it is interrupted by numerous foliar gaps, The segments of the stelar tube are, in this case, individually surrounded by phlœotermal sheaths. In the older region of the hypogæous stem, it becomes continually more difficult to distinguish the phlœoterma on account of the sclerification of the pericycle, and, ultimately, of the phlœoterma itself.

The young stem of *A. cylindrica* has also been studied in this connection, but in this species, even the outer phlœoterma is very poorly developed, and the internal one is obsolete throughout. The absence of a well-marked phlœoterma in the hypogæous stems of the genus Anemone has been especially noted by Janczewski,[44] and accordingly, it is not surprising that this feature should be exemplified by *A. cylindrica.*

The writer has also examined the stem of the closely allied genus Hepatica. In the seeding of *Hepatica triloba,* there is a well-marked external phlœoterma, but the internal phlœotermal sheath is not differentiated at all on account of the sclerification of both the pericycle and the external layer of the medulla. The latter features may be seen in photograph 30, plate 11.

In connection with the Ranunculaceæ may be described the structure of the young stelar system of *Sarracenia purpurea.* In this species, the young central cylinder is tubular with foliar lacunæ. The external phlœoterma is poorly developed and the corresponding internal layer cannot be distinguished even in the very young axis.

The reader who has followed the descriptions given in the foregoing

42 Op. Cit., p. 56.

43 Op. Cit., p. 62.

44 Op. Cit., p. 3.

paragraphs of the development of the stelar system of Ranunculus and Anemone, will doubtless be struck with the bearing of the facts there described, on the problem of the morphology of the central cylinder in the Angiosperms. For example, we find in this order that the astelic type of Van Teighem does not originate by the sinking in of the phlœoterma around the individual bundles, with a subsequent union of the individual phlœotermal sheaths to form a continuous external and internal phlœoterma, because the fibro-vascular system is, from the very first, tubular, and the central cylinder has primitively an internal phlœoterma. Further, the stelar system of so-called monostelic species of Ranunculus and Anemone appears from a study of the course of development to be really an astelic type, in which the internal phlœoterma has become obsolete. These two facts, *viz.*, the primitively tubular (gamodesmic) nature of the central cylinder in the Ranunculaceæ, and the derivation of the so-called monostelic medullated type by the degeneration of the internal phlœoterma, are, in the writer's opinion, of great importance in connection with the view to be taken of the morphology of the central cylinder in the Angiosperms generally. Before proceeding to consider that subject, however, it will be well to describe the development of representatives of other angiospermous groups, which present the phenomenon of astely, so-called.

NYMPHÆACEÆ.

In his essay on Polystely, Van Tieghem describes the Nymphæaceæ as an order illustrating his astelic type of central cylinder. The arrangement of the fibro-vascular strands in the mature stem of the various genera of this order is extremely complex, and, on that account, it is the more desirable to investigate the development of the stelar system in the young plant in order to discover, if possible, what is really the primitive condition of the fibro-vascular apparatus in this group.

The genus Brasenia is probably one of the most primitive of the order. In the internodes of the rhizome of the mature plant of *Brasenia purpurea*, there are present two concentric fibro-vascular strands, in which the elements of the xylem, as is commonly the case in aquatics, are represented merely by air-spaces. The epicotyledonary stele of the seedling of *Brasenia purpurea* is a pithless fibro-vascular strand, in which the vessels are not degenerate as in the mature rhizome. The stelar system retains the simple character until a considerable number of leaf-traces have been given off. The stem, however, sooner or later becomes relatively massive, and the fibro-vascular system

becomes tubular, as in the young stems of the ranunculaceous species described above. The tube has, likewise, both an internal and external phlœoterma, and the stelar tube is characterized by the same foliar gaps, around the margins of which the internal and external phlœotermas communicate. When the young stem has reached a length of from four to eight centimetres, the foliar gaps begin to overlap, and the two concentric strands which are at present in the mature stem make their appearance. When the stem passes out of the mud into the water to form the well-known floating shoots, the xylem degenerates and is represented merely by a cavity in each of the two stelar strands. Photograph 22, plate 10, represents a section through the young tubular stelar system of *Brasenia purpurea*, at a point where a leaf-trace is being given off, and is subtended by its corresponding foliar gap. It will be obvious from the above description and the accompanying photograph that the young stelar system of *Brasenia purpurea* is primitively tubular.

Two species of Nuphar have also been examined in this connection. *Nuphar luteum*, var. *Kalmianum*, is very favorable for study on account of the relative simplicity of its stelar system. The young epicotyledonary central cylinder is here also, at first, a pithless strand, and only after the exit of several leaf-traces does it become tubular with a pith of fundamental tissue. The stelar tube is provided with an internal as well as an external phlœoterma. Photograph 22, plate 10, represents a section through the young rhizome at a point where a leaf-trace has just been given off and a second one is in the act of making its exit from the tubular central cylinder. In the older rhizome, the foliar gaps begin to overlap, so that in a transverse section the stelar tube seems to be broken up into two or more segments, each surrounded by its own phlœotermal sheath. The number of fibro-vascular segments become subsequently increased by the fact that several leaf-traces are given off to each leaf. Finally the stelar tube becomes entirely unrecognizable by reason of the increasing complexity in the arrangement of the vascular strands.

The stelar development of *Nuphar advena* is very similar to that of the species just described. In this case, the epicotyledonary fibro-vascular strand passes quite rapidly into the tubular condition. The fibro-vascular cylinder has likewise internal and external phlœotermas which communicate through the foliar gaps. Very soon the leaf-traces to the individual leaves become numerous, and the stelar tube is consequently interrupted by a large number of foliar gaps. The complexity is subsequently further increased by the appearance of an

internal and external series of strands, and the stelar tube can no longer be recognized as such. Photograph 23, plate 10, represents a section of the young stem of *Nuphar advena* in a region where the leaves have numerous traces and the stelar tube, as a consequence, is broken into many segments.

The young stelar system of *Nymphæa zanzibarensis* is at first a pithless strand, but very rapidly becomes tubular with usual foliar gaps. Quite early all semblance of the original stelar tube vanishes on account of the appearance of complexly anastomosing internal and external systems of fibro-vascular strands.

The young stem of *Nymphæa tuberosa* has also been studied by the writer. The epicotyledonary central cylinder is originally pithless, as in the other nymphæaceous species already described, but rapidly expands and almost immediately breaks up into an extremely complex system of anastomosing bundles, so that it is extremely difficult to recognize the existence of a stelar tube. Towards the end of a season's growth, however, the stelar tube again becomes obvious in the more slender region of the stem which is formed during the autumn. The stelar tube in this case has an internal phloëm as well as an internal phlœoterma. The tubular condition is probably to be regarded as a reversion to the primitive type of stelar system, and may be compared with that noticed by Gwynne-Vaughan[45] in the autumnal region of the stem of *Primula obtusifolia* and *P. involucrata*. In another essay this writer[46] has described the occurrence of concentric fibro-vascular strands in slender pedicles of the tubers which are so characteristic a method of vegetative reproduction in this species. I have examined the structure of the pedicles in question and have confirmed the existence of the concentric strands described by Gwynne-Vaughan. The fibro-vascular tissues in this case form a tube with foliar gaps, a fact which seems to have escaped his notice. As the slender pedicle passes into the tuber, the tubular concentric stele vanishes in an extremely complex system of anastomosing strands, some of which are concentric while others are merely collateral. The reappearance of the tubular stelar system, in the autumnal region of the young rhizome and in the pedicles of the tubers is interesting as a probable case of reversion. The base of the lateral shoots of the rhizome of *Pteris aquilina* not unfrequently shows a reversion to the more primitive tubular stele with a single medullary strand. The writer has found a similar concentric tubular stelar system in the pedicles of *Nymphæa dentata*.

45. Op. Cit., p. 309.

46. Ann. Bot., v. 10, p. 290.

Through the kindness of Mr. Jackson Dawson, of the Arnold Arboretum of Harvard University, the writer has had the opportunity of studying the anatomy of a number of seedlings of *Nelumbium luteum*. The first root in this species is abortive, so that in a series of sections through the base of the young plant, one passes almost immediately into the cotyledonary region. The very short, pithless central cylinder of the young axis becomes tubular immediately below the level of exit of the cotyledonary traces. The exit of the latter breaks the stelar tube into four segments. Photograph 10, plate 8, shows the disposition of the stelar system just above the point where the cotyledonary traces have passed off. One cotyledon, *cot.*, is present; the other has been broken off. The four cotyledonary traces anastomose outside the lacunar cortex and the resulting network gives off the cotyledonary strands proper, as well as a series of strands which run through the cortex of the first internode. Photograph 24, plate 10, represents a section through the first internode; *a* are the four primitive fibro-vascular strands; *f* are the cortical strands. At the second node, the four central strands again form a tube from which a number of functional roots are derived, as well as strands for the third leaf. The exit of the latter causes a breaking up of the stelar tube once more into segments, which are henceforth more numerous than four. The cortical strands likewise send off contributions to the third leaf; they have, however, no connection with the strands of the roots originating from the second node. The latter, as is the rule in both Cryptogams and Phanerogams, unlike the leaf-traces, do not subtend any gaps in the original central cylinder.

MONOCOTYLEDONS.

The orders hitherto discussed belong to the dicotyledonous Division of the Angiosperms. Astely so-called is of comparatively rare occurrence in the present group for reasons which will be subsequently suggested. In this division, as well as in the Dicotyledons, a study of the development of the stelar system seems to throw considerable light on its morphology. The writer does not propose in the present memoir to more than touch on the development of the central cylinder in the Monocotyledons, because that subject appears to him to be of great importance from the standpoint of the phylogeny of the group at present so much in dispute, and for that reason it seems advisable to devote a special memoir to the development of representatives of the various monocotyledonous orders.

Van Tieghem mentions *Pistia stratiotes* among the Aroids as possess-

ing an astelic central cylinder. The writer has been able to confirm the existence of individual phlœotermal sheaths about the fibro-vascular strands in this species; but, unfortunately, in the young plants available, the older region of the stem had already disappeared. Van Tieghem[47] does not give any account of the development of the cauline axis of Aroids in his well-known memoir on the anatomy of the order.

In *Calla palustris*, the young epicotyledonary stele is pithless until after the exit of the second leaf-trace (including that of the cotyledon); just below the point where the fibro-vascular supply of the third leaf is given off, the central cylinder becomes tubular. The traces of the cotyledon and the first leaf are single; but three bundles pass out into the petiole of the third leaf. The three traces of the third leaf subtend three foliar gaps in the central cylinder, which usually close at the fourth node. A continuous fibro-vascular tube thus appears at the node of the seedling similar to that figured by Van Tieghem[48] as occurring at the nodes of the mature rhizome. Above this node the fibro-vascular cylinder is perforated again by gaps corresponding to traces of the fourth leaf, which are likewise three in number. The writer has had the opportunity of following the development of this species in specimens of not more than six nodes. The traces of the sixth leaf are three in number, as are those of the third, fourth and fifth. From the level of exit of the traces of the third leaf, the fibro-vascular cylinder is astelic in Van Tieghem's sense. The fundamental tissue forming the core of this cylinder is at this stage not traversed by any so-called medullary strands, so that the young central cylinder in this species closely resembles that of a Dicotyledon such as *Ranunculus acris*. The individual strands are likewise in the young plant collateral, and the so-called amphivasal concentric strands make their appearance subsequently, as the writer has been able to learn from somewhat older seedlings, which had already lost the primary region of their stems.

The base of the young shoot in *Symplocarpus fœtidus* is tuberous, as is often the case in the Aroids. Photograph 11, plate 8, represents part of the ring of fibro-vascular bundles as it appears about half a centimetre above the base of the tuber. The individual bundles are collateral at this stage, and by treating sections with strong sulphuric acid, the presence of a cutinized phlœoterma may be demonstrated. The phlœoterma appears in the form of sheaths surrounding the separate bundles and hence the fibro-vascular cylinder in this phase of development is astelic. If a section be made through the young axis in the region where the

47 Ann. Sci. Nat. Bot., 5 ser., 6 tom. Recherches sur la Structure des Aroïdé...

48 Op. Cit., plate 4, fig. 5.

tuber passes over into the narrower cylindrical stem characteristic of the older plant, a single circular series of collateral bundles can still be observed. If the sections through this region be treated with sulphuric acid or with phloroglucin and hydrochloric acid, it may be demonstrated that the bundles are no longer surrounded by individual phlœotermal sheaths, but that a single lignified external phlœoterma surrounds the whole complex of bundles. There is present in this species a state of affairs comparable to that already described as occurring in the young stelar system of *Ranunculus rhomboideus*, *viz.*, a primitive so-called astelic condition followed by medullated monostely resulting from the degeneration of the internal phlœoterma. The gaps between the bundles in this stage may be compared with those subtending the subsidiary smaller leaf-traces of many Ranunculaceæ; for in the case of the latter, the fundamental tissues of the pith and of the cortex do not communicate through the foliar gaps because these are so exiguous that they are filled up by the pericycle flanking the adjacent fibro-vascular segments. In *Symplocarpus fœtidus*, the gaps are consequently patent in the thick tuberous base of the primary axis, but in its narrower subsequent cylindrical portion they are occluded by the encroachment of the pericycle on the reduced interval between the fibro-vascular strands. The foliar gaps are, nevertheless, morphologically indicated by the lacunæ in the fibro-vascular cylinder, filled with pericycle, which subtend each and all of the leaf-traces, no matter how small. Not far above the region of transition already described, the central cylinder becomes modified by the appearance of medullary strands and the fibro-vascular bundles become forthwith amphivasal. Photograph 12, plate 8, reproduces the appearance of the central cylinder in a section passing through the cylindrical axis about half a millimetre above its junction with the basal tuber; *e* is the external phlœoterma; *a* are the peripheral bundles, and *b* are leaf-traces which have begun to run in the medulla in the characteristic monocotyledonous fashion.

In *Zea mais* the epicotyledonary stele is a continuous cylinder of fibro-vascular tissue throughout the first internode, which is generally two or three centimetres in length. There is a single gap in the side of the cylinder throughout the internode corresponding to the trace of the cotyledon or scutellum. Above the second node, the fibro-vascular tube is perforated by a large number of foliar gaps, and the leaf-traces corresponding to these immediately pass into the medulla, and pursue henceforth the course so characteristic of the foliar strands in the monocotyledons. There is a well-marked external lignified phlœoterma and a less well-marked and somewhat interrupted internal

phlœotermal sheath. The external and internal phlœotermas apparently do not unite through the foliar gap corresponding to the cotyledonary trace, probably for the reason that the latter is plugged with pericycle.

The writer believes it inadvisable at the present time to enter further into the subject of the development of the central cylinder of the monocotyledons, since it is somewhat complex and specialized, and, moreover, presents a number of interesting features which merit a separate consideration.

CONCLUSIONS.

As a preliminary to the description of his own observations on the anatomy and development of the vegetative axis in the Angiosperms, the writer has suggested certain questions to be answered by a renewed investigation of the facts. It is now in order to discuss how far the study of development and the re-examination of the anatomy of the central cylinder of the Angiosperms recorded in the preceding pages, elucidate the problems suggested in the introduction.

I.—The first question concerns the accuracy of Van Tieghem's description of the mode of origin of his polystelic type of central cylinder. As has been already stated, he regards the polystelic arrangement of vascular strands as the result of the repeated bifurcation of the primary stele. If the writer's observations on the development of the central cylinder in the Filicales as exemplified by his description of the stelar development of *Pteris aquilina*, are correct, the vascular axis in Van Tieghem's polystelic type develops as a concentric fibro-vascular tube perforated by gaps corresponding to the points of exit of the leaf-traces. There is consequently no indication whatever of the repeated forking of the primary stele. In the case of the polystelic Angiosperms, the writer's observations on the Primulaceæ, Halorhagidaceæ and Saxifragaceæ, as well as those of Gwynne-Vaughan on the Primulaceæ, go to show that here also there is no indication of the repeated bifurcation of the epicotyledonary stele, but that the latter gives rise to a tubular central cylinder characterized by lacunæ subtending the points of exit of the foliar strands. It would appear that Van Tieghem has failed to notice the extremely important influence of the leaf-traces on the conformation of the central cylinder in the Filicales and Angiosperms. Had he devoted more attention to the subject of development, this important feature could hardly have escaped his observation.

The writer has already referred to the inadequacy of Van Tieghem's conception of the so-called polystelic type. It seems inappropriate to designate the young tubular central cylinder of *Pteris aquilina* and *Primula auricula* as gamostelic, since the use of this term implies Van Tieghem's conception of the repeated bifurcation of the primary stele and the subsequent union of the fractions to form a stelar tube. The study of development shows the tubular condition to be in reality primitive and the writer[49] has, previously, in view of that fact, suggested that this form of central cylinder be designated siphonostelic.

The studies of Gwynne-Vaughan and of the writer on the Primulaceæ, Halorhagidaceæ, and Saxifragaceæ seem to show that the siphonostelic type of central cylinder, with internal phloëm, is not to be regarded as primitive in the case of the Angiosperms, but that it is derived from a siphonostelic type in which there is primitively no internal phloëm. This conclusion is justified by the fact that the *young* stelar tube is sometimes actually without internal phloëm, *e.g.*, *Primula japonica*, *P. farinosa*, and *Gunnera scabra*, and by the fact that, even when the young stelar axis is concentric from the first, the leaf-traces retain the apparently ancestral collateral type, *e.g.*, *Primula Auricula*. Gwynne-Vaughan attributes the appearance of internal phloëm in the central cylinder of certain Dicotyledons to an effort to make up for the loss of a cambium, a feature correlated with so-called polystely.

II.—The writer's study of the development of the so-called astelic central cylinder of certain Ranunculaceæ and Nymphæaceæ shows that in this type, the course of events is practically the same as that in the so-called polystelic axis, *viz.*, that the epicotyledonary stele becomes in the young plant a tube interrupted by foliar gaps. The tubular character of the stelar system may be subsequently disguised by the increasing complexity of the arrangement of the fibro-vascular strands, but in all such cases the collateral stelar tube may be recognized in the young axis. The writer has not been able to find any evidence in the facts of stelar development in seedlings, supporting Van Tieghem's statement that his astelic type originates by the separation of the phlœoterma into segments, which unite around the individual bundles Neither do his observations accord with the more recent description given by Van Tieghem[50] of the astelic type, in which he states that astely or schizostely as he now prefers to call it (adopting a suggestion of Strasburger's), originates by the stele breaking up into as many meristeles as it contains bundles. The young stele in these cases is

49. Trans. Brit. Ass. Adv. Sci., 1897, p. 869.

50. Éléments de Botanique, p. 179.

always a continuous hollow cylinder of fibro-vascular tissue, bounded internally and externally by phlœotermal sheaths, which communicate through the foliar lacunæ, and is in fact primitively of the conformation described by Van Tieghem as gamodesmic or gamomeristelic. The use of these terms, however, seems inappropriate, since they imply the union of bundles or meristeles originally separate. The writer has suggested the term siphonostelic as fitly describing the stelar type occurring in the stem of *Pteris aquilina* or *Primula farinosa*. The question may now be asked whether this term should not also be applied to the very similar stelar conformation found in the Ranunculaceæ and Nymphæaceæ. The most striking difference between the stelar systems of the two types is the absence of an internal phloëm in the case of the Nymphæaceæ and Ranunculaceæ. But Gwynne-Vaughan has called attention to the fact that the collateral fibro-vascular strands of the Nymphæaceæ often become concentric, an observation which the present writer has been able to confirm. On the other hand, the siphonostelic central cylinder of *Primula japonica* and *P. farinosa* starts as a collateral stelar tube, only subsequently becoming more or less completely concentric. In the floral axes of these species, moreover, both the internal phloëm and the internal phlœoterma disappear, giving rise to a central cylinder, which, if its mode of origin had not been followed, would be regarded as medullated monostelic. The flowering stems of all the described species of so-called polystelic Primulas have the same peculiarity. It has been shown in the earlier part of this essay that the stelar strands of *Parnassia palustris*, within an interval of a fraction of a millimetre, may be successively collateral and concentric, while in *P. parviflora* the cauline strands are collateral and the leaf-traces concentric. The two types of fibro-vascular strand pass imperceptibly into each other in the Angiosperms, and, as will be subsequently shown, also in the Gymnosperms and the Vascular Cryptogams. It would appear from the study of development that Van Tieghem's polystelic and astelic types are essentially the same, inasmuch as the stelar system in both cases is primitively a tube with foliar lacunæ. Further, the presence or absence of internal phloëm appears to be a matter of slight morphological importance.

III.—We may now pass to the question of the morphology of the medullated fibro-vascular axis, bounded by an external phlœoterma only. It has already been pointed out that Van Tieghem regards the central cylinder in this type as derived from the pithless stele of the hypocotyl, by dilatation and the formation of a parenchymatous medulla, differing morphologically from the fundamental parenchyma outside the stele. It has also been mentioned that Van Tieghem considers that his medullated monostelic type of central cylinder, and his astelic type, may

co-exist in different species of the same genus. For example, *Ranunculus aquatilis* is, according to his view, astelic, and *R. abortivus* is, on the other hand, medullated monostelic. Strasburger has questioned the possibility that the pith in different species of Ranunculus should be sometimes extrastelar (in the astelic type), and intrastelar (in the monostelic type). He prefers to consider that the medulla is always intrastelar, and that, consequently, the individual endodermal sheaths in the species of Ranunculus, where they occur, are different morphologically from the phlœoterma, which he supposes surrounds the complex of bundles in the so-called medullated monostelic types.

The writer's examination of the development of a number of species of Ranunculus and Anemone has shown that in the young axis the stelar system possesses an internal phlœoterma which is continuous with the external phlœoterma through the foliar gaps, and is therefore of the same morphological value. In some species the internal phlœoterma disappears in the older region of the stem, *e.g.*, *R. abortivus* and *R. rhomboideus*, and the stelar axis then appears to be monostelic. A study of its development, however, shows that it is primitively astelic.

This view of the matter quite removes the difficulty of having to regard the pith in some species of Ranunculus and Anemone as intrastelar and in other species as extrastelar, because their ontogeny shows that the pith is in both cases extrastelar, *i.e.*, ordinary fundamental tissue which has been enclosed by the stelar tube. In the older stem of various species of Ranunculus and Anemone, both external and internal phlœotermas disappear when there is much sclerenchymatous tissue present in the vascular system. It is probably not going too far to state as a result of the study of development that in the genus Ranunculus the pith is throughout extrastelar. In consequence of his detailed anatomical study of the order Ranunculaceæ, Marié[51] has come to the conclusion that the genus Ranunculus is the stock from which all the other genera of Ranunculaceæ have taken their origin. It will probably not be an easy matter to demonstrate the existence of an internal phlœoterma even in the young stems of the various ranunculaceous genera, especially where there is much sclerification of the central cylinder or much secondary growth, since even the external phlœoterma under these circumstances is nearly always with difficulty distinguishable. It is not unlikely, however, that the internal phlœoterma will be found to persist in the more conservative vascular system of the floral axes. In any case, there appear to be

51 Op. Cit., p. 108.

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better reasons for regarding the Ranunculaceæ throughout as astelic, in Van Tieghem's sense, than as entirely medullated monostelic, according to Strasburger, or in part medullated monostelic, and in part astelic, according to Van Tieghem.

If the central cylinder of the Ranunculaceæ be throughout collateral siphonostelic in the sense described by the writer, it would seem necessary to extend that conception of the morphology of the central cylinder to the rest of the dicotyledonous Angiosperms. It appears highly probable that an exhaustive study of seedlings and floral axes of representatives of the various orders will result in the discovery of a number of facts favorable to this view, and an investigation in this direction is in progress.

The writer's observations on Monocotyledons point to the same general conclusion, although here the reduction in size of the foliar lacunæ and the high development of the pericyclic mechanical tissues which has brought this division into special prominence in connection with Schwendener's mechanical theories, make the demonstration of an internal phlœoterma much more difficult. The Aroids have been chosen to illustrate preliminarily the fundamental astely of the Monocotyledons. *Calla palustris* is throughout astelic in Van Tieghem's sense; *Symplocarpus fœtidus* is obviously astelic in the young stem, while in the older axis it is apparently medullated monostelic, on account of the degeneration of the internal phlœoterma. We may preliminarily assume that the Aroids have throughout a pith derived from the fundamental tissues. This conclusion may be extended to the other Monocotyledons and it may be further stated that the primitive stelar condition in the Monocotyledons is tubular, and that the central cylinder is interrupted by foliar lacunæ corresponding to the leaf-traces. The peculiar cauline course of the bundles in the Monocotyledons is not primitive, since it does not appear in the young stem.

Taking into consideration all the facts derived from a study of the Angiosperms, the general statement may be made that the primitive type of stelar system in the group is a hollow fibro-vascular tube with gaps corresponding to the leaf-traces. This type of stele may appropriately be called siphonostelic. In siphonostelic axes the stelar tube may have both internal and external phloëm, and this case may conveniently be described as amphiphloic. Where the internal phloëm is absent, as is the case in the majority of the Angiosperms, the stelar tube is ectophloic. The pith is always to be regarded as merely an included portion of the fundamental tissues.

In the reduced central cylinder of certain angiospermous species of aquatic or amphibious habit, the stelar system has become contracted on account of the correlated degeneracy of the vascular elements. In these cases, the parenchymatous core in the centre of the stele, *e.g.*, that of *Parnassia palustris*, represented in photograph 25, plate 11, is to be regarded as included pericycle, morphologically similar, for example, to that found in the *young* fibro-vascular axis of *Primula farinosa*. The contracted central cylinder in such cases, is none the less to be regarded as essentially siphonostelic, although it has no true medulla.

IV.—We may now ask if the study of the development of the central cylinder in the Angiosperms supplies any morphological facts which are of phylogenetic value. Attention has already been directed to the primitively tubular character of the central cylinder throughout the Angiosperms. It has been furthermore noted that the stelar tube is characterized by foliar gaps corresponding to the traces of the leaves. It is of interest to discover whether the occurrence of foliar lacunæ is constant, or whether it is in any way influenced by environment. The Cactaceæ and the amentiferous genus Casuarina present perhaps the most extreme cases of foliar reduction among the Angiosperms, and it is of interest to discover whether the foliar gaps are obsolete in these examples. The writer has satisfied himself by examination of species of Opuntia and Cereus, of the accuracy of Ganong's[52] statement as to the occurrence of gaps in the fibro-vascular system of the Cactaceæ, corresponding to the extremely reduced leaves. The stelar system of seedlings of *Casuarina equisetifolia* grown from seeds obtained from Kew, is also characterized by the presence of well-marked foliar gaps. It may consequently be assumed that the occurrence of foliar gaps is a constant characteristic of the Angiosperms.

The possession of an essentially tubular stelar system interrupted invariably by foliar gaps appears to be a palingenetic feature of the Angiosperms. In this group there are so few anatomical characters which can rank as phylogenetic criteria that the demonstration of an additional one may be expected to contribute something to the solution of the extremely difficult problem of its origin.

In an earlier memoir,[53] the writer has called attention to the value of a study of the stelar system in connection with the phylogeny of vascular Plants. It would indeed be strange if an apparatus so characteristically separating them as a whole from the lower Cryptogams did not

52 Beitrag. Z. Kennt, d. Morph, u. Biol. d. Cacteen. Inaugural. Dissertation, p 13 etc.

53 Mem. Boston Soc. Nat. Hist., Vol. 5, No. 5.

manifest some features of phylogenetic importance. The writer has pointed out that siphonostely exists under two modifications among the vascular Cryptograms, *viz.*, siphonostely, in which the gaps of the stele correspond to leaf-traces; and siphonostely, in which there are no foliar gaps, but in which the stelar lacunæ correspond to branches. He has designated the former type phyllosiphonic; the latter, cladosiphonic. The use of this distinction, together with all other available characteristics, results in the placing of the Lycopodiales and Equisetales near one another in the system as groups which are invariably cladosiphonic. The Filicales, Gymnospermæ, and Angiospermæ, on the other hand, are uniformly phyllosiphonic. The writer does not intend to go further into this matter in the present memoir, but it may nevertheless be suggested that there are two distinct primitive groups of vascular plants, *viz.*, the Lycopsida and the Pteropsida. To the former group belong the Lycopodiales and Equisetales; to the latter, the Filicales, the Gymnospermæ, and Angiospermæ. The validity of the classification indicated above, in the case of Lycopsida, has already been discussed by the writer,[54] in his memoir on the genus Equisetum. The considerations which favor the setting up of the other great alliance can be more advantageously examined subsequently.

V. If the writer has correctly interpreted the anatomical facts described and figured in the present memoir, the morphological ideas of Van Tieghem can no longer be accepted in full. It is the great merit of that distinguished botanist to have recognized in so large a measure the essential unity of the fibro-vascular system of plant axes. That he should have gone too far in the direction of unity in the case of the so-called medullated monostelic type, and not far enough in his polystelic type, is to be explained by the comparatively slight attention given by him to the subject of development. Strasburger, in respect to monostely, has gone even further than Van Tieghem, for he unites Van Tieghem's astelic type with the medullated monostelic, and regards the medulla in both cases as intrastelar parenchyma. An examination of the anatomy of the young axis apparently brings us back to the standpoint of De Bary in regard to the morphology of fibro-vascular strands. The older anatomist, however, on account of his intentional neglect of ontogeny, appears to have completely overlooked the morphological unity of the cauline fibro-vascular apparatus of the Angiosperms.

Since it is impossible to investigate experimentally any but the

[54] Mem. Boston. Soc. Nat. Hist., Vol. 5, No. 5.

smallest morphological problems, all interpretations of the greater questions of morphology must ever remain more or less hypothetical. The persistent recurrence of a tubular stelar system throughout the various groups of vascular plants suggests that the tubular arrangement of the primitive skeletal tissues is often an advantage. The nature of the advantage is apparently not far to seek. One important function of plant axes is to afford support to their appendicular organs, and we may regard the tubulization of the stele as an adaptation for this purpose. Where the mechanical function is taken on by the extra-stelar tissues, siphonostely is often absent or degenerate. Further, those organs of plants which are normally supported by the soil, viz., the roots, are not primitively siphonostelic at all, and in the comparatively rare cases where their central cylinder is medullated, its parenchyma is derived from the pith of the stem. The truth of the latter statement will be more apparent when the development of the stem in certain Filicales has been described. It would consequently appear that the tubular fibro-vascular cylinder, which is so characteristic of the cauline axis of the Angiosperms, is the result of the operation of mechanical causes, and that the anatomical peculiarities which distinguish the primary central cylinder of the root from the stelar tube of the shoot are primitive features, retained undisturbed by the mechanical influences acting on the stem.

SUMMARY OF RESULTS AND CONCLUSIONS.

1. The polystelic type of Van Tieghem is not characterized by the repeated bifurcation of the epicotyledonary stele, but there is primitively in the young stem of this type a tubular concentric stele with foliar gaps subtending the points of exit of the leaf-traces.

2. The astelic type of Van Tieghem does not result from the separation of the epicotyledonary stele into its constituent bundles; for in the young so-called astelic axis, there are no bundles present at all, but a collateral stelar tube with foliar gaps subtending the leaf-traces, through which the internal and external phlœotermal sheaths communicate.

3. The medullated monostelic type of Van Tieghem does not originate, as he states, by the dilatation of the epicotyledonary stele and the formation of an *intrastelar* pith; for the writer's observations show that in favorable cases, both among the Dicotyledons and the Monocotyledons, the so-called medullated monostelic central cylinder of the older stem may be seen to be derived from the so-called astelic condition of the *young* axis, by the degeneration of the internal phlœoterma.

4. Van Tieghem's three types of central cylinder indicated above are all merely modifications of a single type, which has been designated by the writer, siphonostelic. In this type the central cylinder is primitively a fibro-vascular tube with foliar lacunæ opposite the points of exit of the leaf-traces. In the so-called polystelic modification, the central cylinder has internal, as well as external phloëm, and may be described consequently as amphiphloic. In the astelic type of axis so-called, the internal phloëm is absent and the central cylinder is accordingly to be designated ectophloic. The medullated monostelic type of Van Tieghem is derived from the last-named by the degeneration of the internal phlœoterma or endodermis.

5. The siphonostelic type of central cylinder as defined above is probably to be regarded as the result of the mechanical strengthening of the cauline axis to enable it to support the palingenetically large leaves which are characteristic of the Angiospermæ, Gymnospermæ, and Filicales. In these three groups, the siphonostelic, fibro-vascular cylinder is invariably distinguished by the presence of gaps corresponding to the points of exit of the leaf-traces, and, in this feature, offers a marked contrast to the tubular central cylinder of the Lycopodiales and Equisetales, in which there are no foliar lacunæ, but, on the contrary, gaps subtending the branches.

6. A study of the development and structure of the fibro-vascular apparatus of the various groups of vascular plants is likely to throw considerable light on their phylogeny and to elucidate the causes of the morphological differences in the structure of the central cylinder of root and shoot.

For many kindnesses in the matter of supplying material for this research, the writer wishes to express his obligations to the Director of the Royal Gardens, Kew; to the Director and Assistant Director of the Botanical Gardens of Harvard University; to Dr. D. H. Scott, Honorary Director of the Jodrell Laboratory, Kew, and to Mr. Jackson Dawson, of the Arnold Arboretum of Harvard University. He is specially indebted in this respect to Prof. G. L. Goodale, Director of the Botanical Gardens of Harvard University. Lastly, the writer owes not a little to his assistant, Mr. R. B. Thomson, B.A., for help in securing the seedlings necessary for the present investigation.

DESCRIPTION OF THE PLATES.

PLATE VII.

PHOTOGRAPH 1.—Transverse section of a young stem of *Pteris aquilina*, at the point of origin of the second leaf. (X 40.)

PHOTOGRAPH 2.—Transverse section of the older stem of *P. aquilina*; l^1 and l^2 are leaves; *r* is a root. (X 25.)

PHOTOGRAPH 3.—Transverse section of the stem of *P. aquilina* above the region of forking of the stelar system; *a* and *b* are the two cylindrical steles; *l* is a leaf-trace. (X 15.)

PHOTOGRAPH 4.—Transverse section of the young horizontal rhizome of *P. aquilina*. (X 25.)

PHOTOGRAPH 5.—Transverse section of the older horizontal rhizome of *P. aquilina*. (X 25.)

PHOTOGRAPH 6.—Transverse section of a still older region of the same. (X 25.)

PLATE VIII.

PHOTOGRAPH 7.—Transverse section of young stem of *Primula farinosa*. (X 40.)

PHOTOGRAPH 8.—Transverse section of the older stem of *P. farinosa*; l^1 and l^2 indicate the foliar gaps; r^1 and r^2 are roots. (X 25.)

PHOTOGRAPH 9.—Transverse section of the same stem with same lettering as photograph 8. (X 25).

PHOTOGRAPH 10.—Transverse section of the young stem of *Nelumbium luteum*, at the point of origin of the cotyledons. (X 25.)

PHOTOGRAPH 11.—Transverse section of part of the tuberous region of the stem of *Symplocarpus fœtidus*, showing the so-called "astelic" condition. (X 25.)

PHOTOGRAPH 12.—Transverse section of cylindrical portion of the stem of the same, showing the "medullated monostelic" condition; *e*, phlœoterma; *a*, peripheral strands; *b*, foliar traces. (X 20.)

PLATE IX.

PHOTOGRAPH 13.—Transverse section of the young stem of *Ranunculus acris*. (X 25.)

PHOTOGRAPH 14.—Transverse section of the older stem of *R. acris*. (X 25.)

PHOTOGRAPH 15.—Transverse section of the older young stem of *R. abortivus*. The internal phlœoterma is still perceptible. (X 25.)

PHOTOGRAPH 16.—Transverse section of the older young stem of *R. rhomboideus*. The internal phlœoterma cannot be distinguished. (X. 25.)

PHOTOGRAPH 17.—Transverse section of the young stem of *R. rhomboideus*. The internal phlœoterma is still visible. (X. 25).

PHOTOGRAPH 18.—Transverse section of the young stem of *R. rhomboideus*, showing the communication of internal and external phlœotermal sheaths through the foliar lacuna. (X. 25.)

PLATE X.

PHOTOGRAPH 19.—Transverse section of the young stem of *Anemone pennsylvanica*, showing the presence of an internal phlœoterma. (X. 25.)

PHOTOGRAPH 20.—Transverse section of the older young stem of *A. pennsylvanica*, showing the overlapping of the foliar gap. (X 25.)

PHOTOGRAPH 21.—Transverse section of the young stem of *Brasenia purpurea*, showing the primitively tubular condition of the stelar system. (X. 20.)

PHOTOGRAPH 22.—Transverse section of the young stem of *Nuphar luteum*, var. *Kalmiannm*, showing the tubular stele. (X 25.)

PHOTOGRAPH 23.—Transverse section of the older young stem of *Nuphar advena*. (X 25.)

PHOTOGRAPH 24.—Transverse section of the young epicotyledonary stelar system of *Nelumbium luteum*; *a*, primitive stelar strands; *f*, cortical bundles. (X 25.)

PLATE XI.

PHOTOGRAPH 25.—Central cylinder of *Parnassia palustris*. (X 45.)

PHOTOGRAPH 26.—"Polystelic" phase of central cylinder of *P. palustris*, l^1 and l^2 are leaf traces. (X 12.)

PHOTOGRAPH 27.—Inferior region of "astelic" portion of central cylinder of *P. palustris*. (X 45.)

PHOTOGRAPH 28.—Transverse section of the stele of *P. palustris*, at point of origin of a leaf-trace (X 12.)

PHOTOGRAPH 29.—Transverse section of "astelic" central cylinder of *P. parviflora*, g^1 and g^2 are foliar gaps; *l* is a leaf-trace. (X 25.)

PHOTOGRAPH 30.—Transverse section of central cylinder of the young stem of *Hepatica triloba*. (X 40.)

R. rhomboideus. The
25).

. rhomboideus, showing
al phlœotermal sheaths

Anemone pennsylvanica,
eoterma. (X. 25.)

m of *A. pennsylvanica*,
p. (X 25.)

senia purpurea, showing
elar system. (X. 20.)

f *Nuphar luteum*, var.
(X 25.)

em of *Nuphar advena*.

onary stelar system of
strands; *f*, cortical

5.)

palustris, l^1 and l^2 are

central cylinder of *P.*

s, at point of origin of a

ylinder of *P. parviflora*,
ce. (X 25.)

young stem of *Hepatica*

Fig. 1.

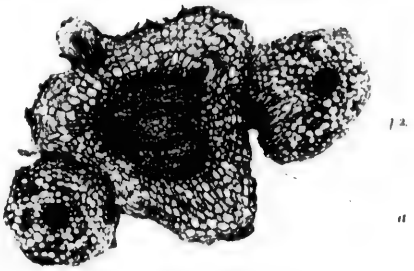
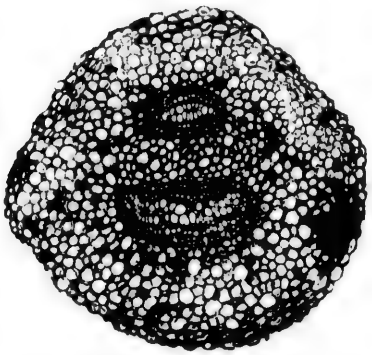


Fig. 2.

Fig. 3.



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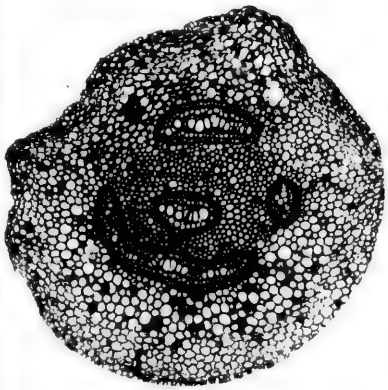

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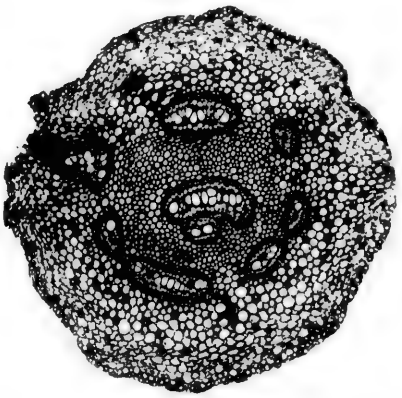

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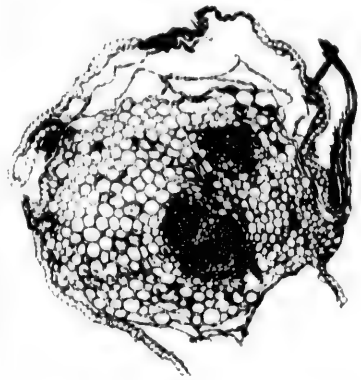

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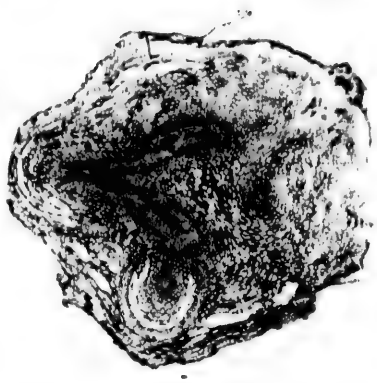

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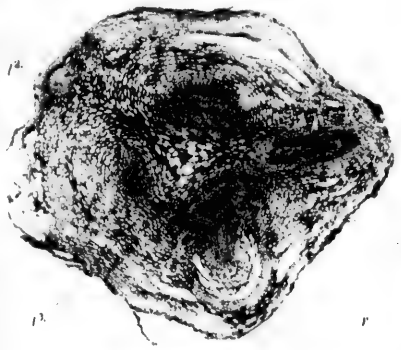

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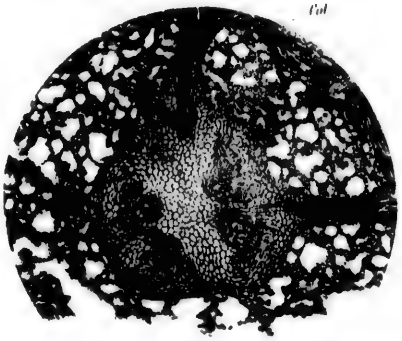

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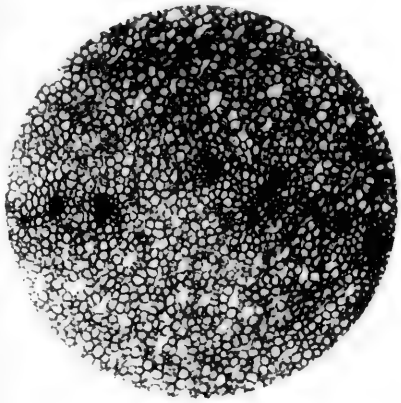

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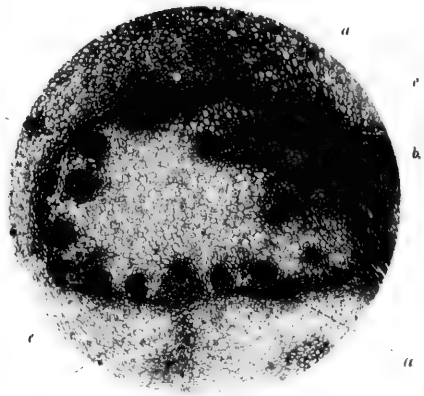

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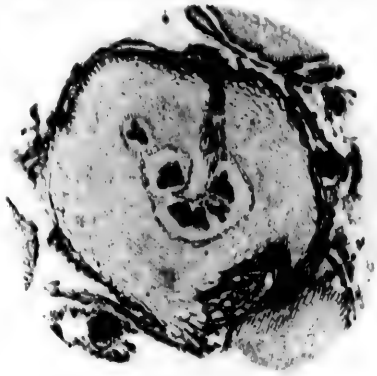

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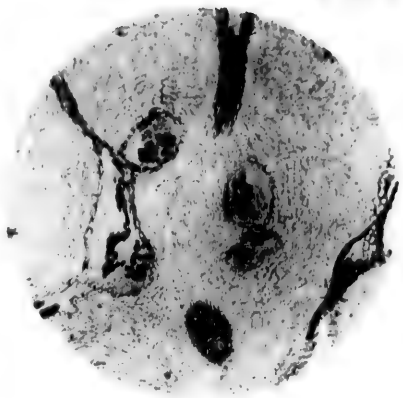

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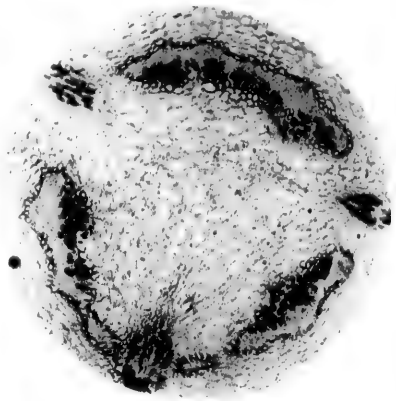

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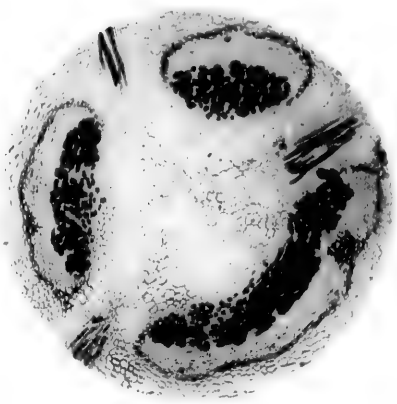

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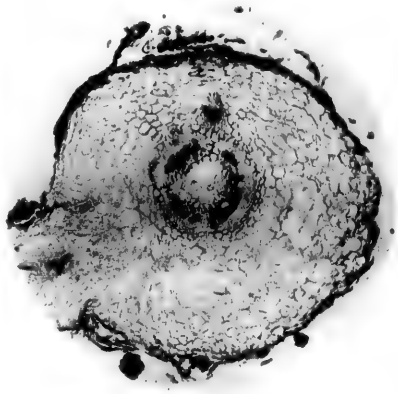

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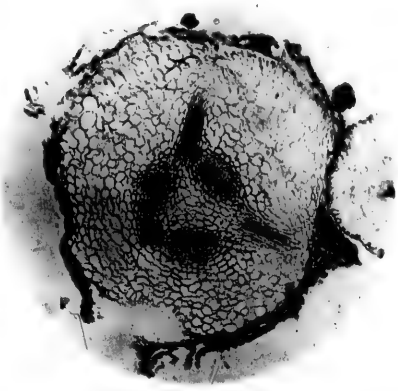

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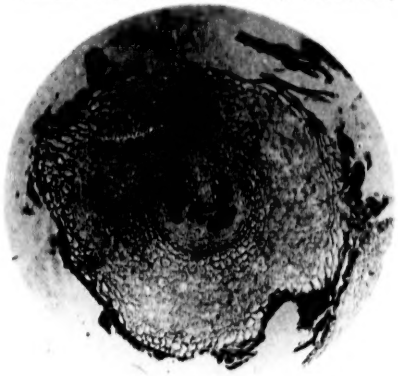
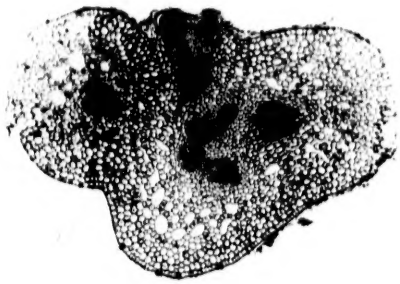


Fig.19.

Fig.20.



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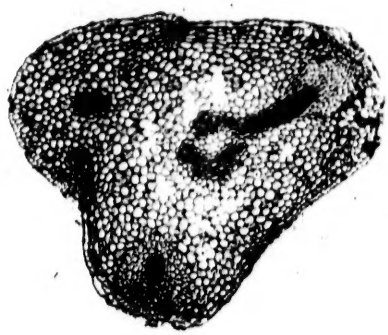
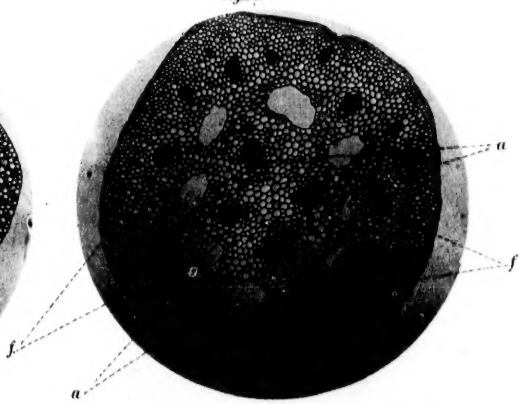


Fig.22.

Fig.23.



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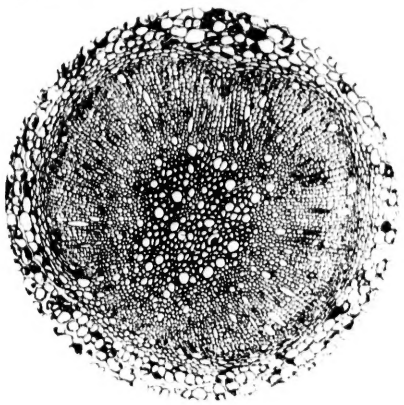

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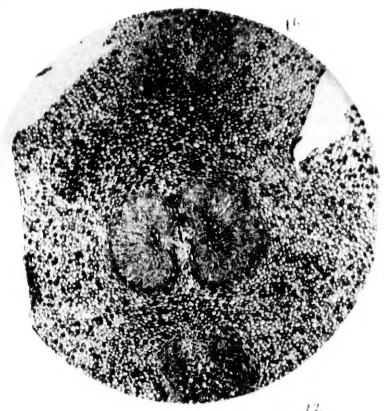

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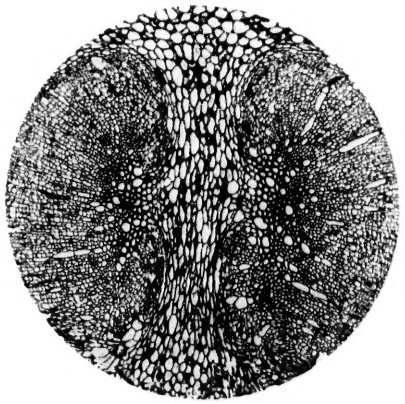

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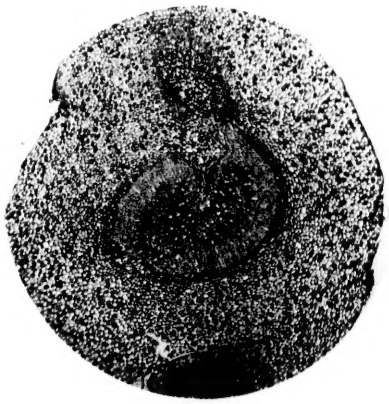

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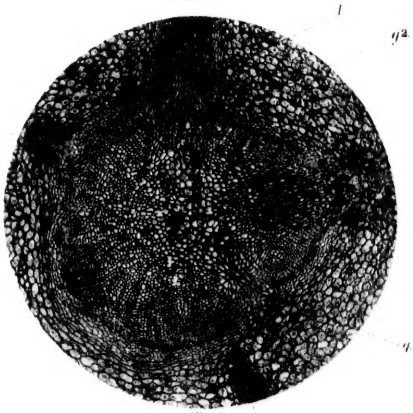

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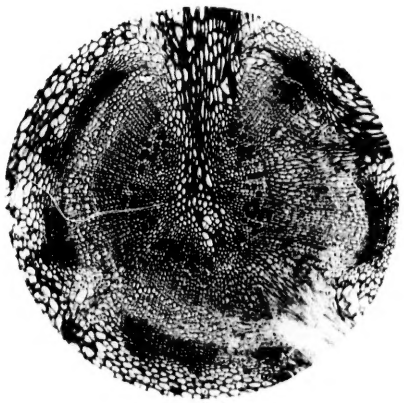

Fig. 30.